Crop Improvement and the Accumulation and Partitioning of Biomass and Nitrogen in Lentil

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ABSTRACT

Domestication and subsequent genetic enhancement in lentil (*Lens culinaris* Medik.) have involved changes in plant structure and DM distribution. These changes were examined using a "genetic gradient" comprising three representatives each of *Lens orientalis* (Boiss.) progenitors, landraces, pre-1980 cultivars, and modern germplasm. All 12 genotypes were sown at Pullman, WA, in 1996 and 1997, and at Reading, UK, in 1997. The biomass (all genotypes) and N concentration (four genotypes) of above-ground tissues were measured at 50% flowering (leaf and stem) and at reproductive maturity (leaf, stem, pod wall and seed). The progenitors produced meager biomass (averaging 0.72 Mg ha^{-1}) and poor HI (0.19), and consequently small seed yields (0.11 Mg ha^{-1}). Productive landraces had substantially higher biomass (3.52 Mg ha^{-1}), improved HI (0.34), and larger seed yields (1.13 Mg ha^{-1}). Biomass and seed yield were increased further by the selection of cultivars (5.11 and 1.32 Mg ha^{-1}, respectively). The development of modern germplasm by hybridization further increased seed yields (1.95 Mg ha^{-1}). Consistent seed yield improvements have not been associated with consistent increases in HI. Instead a strong, positive correlation between seed yield and biomass has persisted. NHI increased more rapidly than HI and is unlikely to increase further in the future. Future seed yield improvement will therefore depend on increased N accumulation. Reliance on N$_2$ fixation must be supported by increased photosynthetic capacity and therefore by vegetative biomass. An advantageous correlation between seed yield and residue production seems likely to persist as crop improvement continues.

THE SEEDS OF LENTIL are an important protein- and carbohydrate-rich food in many developing regions and are becoming increasingly popular in developed countries where they are perceived as a healthy component of the diet (Savage, 1991). Lentil seed yields are small relative to those of cereals: the world average in 1996 was just 0.83 Mg ha^{-1}, i.e., about one-third that of wheat (2.54 Mg ha^{-1}) (FAO, 1997). Despite the traditional use of lentil straw as feed, primarily for sheep and goats in the Middle East, biomass production has not been a conscious selection target for lentil breeders until the last 20 yr (Erskine, 1983; Erskine et al., 1999). However, the increasing need for organic residues to help restrict soil erosion has stimulated interest in the breeding of lentils for biomass production (Whitehead et al., 1998; Erskine et al., 1999). Nowhere is the need for residue production greater than on the slopes of the Palouse region of Washington and Idaho, USA, where about 90 000 Mg of lentils are produced annually (USA Dry Pea and Lentil Council, 1996) and where soil ero-

sion problems are increasingly severe (Küsmenoğlu and Muehlbauer, 1998).

Individual lentil plants are typically short with slender stems and so crop stands produce small amounts of biomass relative to cereals. For example, in independent work done at comparable latitudes, five modern cultivars of winter wheat (*Triticum aestivum* L.) grown at Cambridge, UK, averaged 7.8 Mg straw ha^{-1} (Austin et al., 1989), whereas six lentil cultivars grown over three seasons in Pullman, WA, produced just 1.4 to 3.3 Mg residue ha^{-1} (McPhee et al., 1997). In these latter experiments, 'Brewer', the most widely grown lentil cultivar in the Palouse, produced 1.7 to 2.3 Mg residue ha^{-1}. A further contrast with cereals is that lentil residues are easily fragmented during harvesting and tillage. Consequently, as much as 85% of the residue may be blown away and/or will decay rapidly rather than remaining as fragments in the surface layers of the soil where they are needed to help restrict erosion (McPhee et al., 1997). The difficulties experienced in meeting USDA Natural Resources Conservation Service requirements for surface residues, and thus in maintaining eligibility for federal support, have consequently focused attention on biomass production and management in traditional lentil–wheat cropping systems in the Palouse.

Throughout the past century cereal breeders have sought to increase grain yield primarily through the selection of traits which reduce the incidence of lodging, and hence which permit cereal crops to benefit from increased applications of N fertilizer and assured supplies of water (Austin et al., 1980; Hay, 1995). The incorporation of dwarfing genes in the 1960s increased grain yield potential dramatically while reducing straw production substantially. For example, when cultivars of English barley (*Hordeum vulgare* L.) released in 1900 or 1980 were compared under uniform growing conditions the older ones yielded 4.5 Mg grain ha^{-1} compared with 7 Mg grain ha^{-1} for the modern cultivars (Hay, 1995). Increased seed yield was almost entirely accounted for by increased harvest index (HI; the ratio of the dry weight of grain to that of above-ground biomass) from 0.36 to 0.48. In contrast with cereals, lentil cultivars released prior to 1980 were mostly selections from germplasm rather than the products of hybridization (Hawtin et al., 1980). More recently, breeding programs have successfully produced improved genotypes from lentil hybridization and selection. However, there is cause for concern that the already poor residue productivity of this grain legume crop could be further depressed if, as in cereals, improved seed yields are sought through

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genetic selection for increased HI (Summerfield and Lawn, 1987).

It is typical in annual crops for more than 50% of the N within the leaves to be directly involved in the composition and function of the photosynthetic apparatus (Evans and Seemann, 1989). The patterns of DM and N accumulation in crops in general, and in lentil in particular, are consequently closely synchronized (van Kessel, 1994). Early seedling growth in lentil is dependent upon inorganic (soil or fertilizer) N but once nodules are established, symbiotic N_2 fixation rates increase rapidly and N_2 fixation can account for as much as 85% of the N assimilated throughout the entire duration of the crop (van Kessel, 1994). In many circumstances, then, both biomass and seed yield are closely dependent on seasonal N_2 fixation. The N requirement is especially large during reproductive growth when 28 mg N g^{-1} seed are required by lentil compared with only 16 mg N g^{-1} grain for wheat (Sinclair and de Wit, 1975). However, during the later stages of pod filling, it is usual for N_2 fixation rates to decrease. We (Whitehead et al., 1998) and others (van Kessel, 1994; Kurdali et al. 1997) have interpreted these declines in lentil to reflect competition with developing seeds for photosynthates combined with a declining photosynthetic capacity of an ageing canopy and the onset of adverse environmental conditions such as heat and drought stress. During this period, substantial remobilization of N from vegetative organs into seeds occurs to an extent which can account for as much as 70% of the N in seeds by reproductive maturity (Kurdali et al., 1997).

The present research has examined the consequences of crop improvement on the production of biomass in lentil and on the partitioning of DM and N among seeds, leaves and stems. A "genetic gradient" which begins with wild progenitor accessions and progresses through landraces and older cultivars released before 1980 to modern breeding stocks and recently-released germplasm has been investigated.

MATERIALS AND METHODS

Plant Material

A genetic gradient of lentil genotypes, along which selection for seed yield has progressively intensified, was investigated. It comprised three genotypes from each of four cohorts, viz. wild progenitors (Lo153 from Syria, Lo56 from Turkey and Lo4 from Uzbekistan), landraces (the pre-1960 accessions PI 211732 from Syria, PI 169527 from Turkey and PI 181949 from Afghanistan), older cultivars released in the 1970s (Chilean 78, Tekoa, and Laird) and modern cultivars or breeding lines [LC960254 (released as 'Mason' in 1996), LC460266, and LC460199]. All of the cultivars and two of the landraces (PI 181949 and PI 169527) had large yellow cotyledons. The land race PI 211732 was a heterogeneous seed lot but only smaller seeds with green testas and orange cotyledons were sown. All three *L. orientalis* progenitors had very small seeds with brown testas and red cotyledons, which were scarified prior to sowing in order to improve the rate and percentage of germination.

Plant Husbandry

All 12 genotypes were sown at Pullman, WA, (46° 46′ N, 117° 12′ W) on 9 May 1996 and again on 12 May 1997, and at Reading, UK (51° 27′ N, 0° 0′ W) on 21 March 1997 in a randomized complete block design with three replicate plots per harvest. The soil at Pullman was a fine-silty, mixed mesic pachic ultic haploxeroll of the Palouse Series (McPhee et al., 1997); at Reading it was a brown acid coarse sand over-lying reddish brown coarse sand of the Rowland Series (Kay, 1936). All three experiments were rainfed, although supplementary irrigation was applied shortly after sowing at Pullman in 1997 in order to ensure that adequate soil moisture was available for germination. Daily minimum and maximum temperature and daily rainfall were recorded throughout crop duration for each experiment. All genotypes in all experiments were seeded in four-row plots each 1 m long at a within-row spacing of 5 cm and with 30 cm between rows. At Pullman weeds were controlled by incorporation of Pursuit (Cyanamid, Princeton, NJ)[1] (Imidazolinone, -2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-5-ethyl-3-pyridinecarboxylic acid) prior to sowing. At Reading, no herbicides were used and weeds were removed by hand as and when necessary. No fertilizers or rhizobium inoculants were applied, and healthy nodules were formed on the roots of all genotypes in all sowings. To prevent the loss of seeds from shattering pods, the emerging seedlings of the wild progenitors were threaded through small holes cut into screen netting (mesh size 1 mm²) which covered the soil surface. Shortly before the first pods reached reproductive maturity the netting was unfolded so as to completely cover the plants, thus preventing unquantified seed loss.

At 50% flowering (Stage R1; Erskine et al., 1990), and again at reproductive maturity by which time 90% of the pods were golden brown (Stage R8), 0.5 m of each of the two central rows of each replicate plot of each genotype were harvested by hand cutting at ground level. This left 0.25 m (i.e., 5 or 6 plants) as a border in each row. Experience with these field plot experiments with lentil once again confirms that with plots of these dimensions and sampling protocols there was no evidence of any "border effects" in terms of plant height (shading) or root competition. The respective times to 50% flowering and reproductive maturity (and so by difference the duration of the reproductive period) were recorded for each plot. The dry weights of vegetative material, pods and seeds were determined separately after drying for 48 h at 70°C. To measure the extent to which biomass was lost before harvest, and the growth stage at which these losses occurred, three plots of each of one genotype from each cohort (i.e., Lo153, PI 181949, Chilean 78, and LC460266) were surrounded with netting in order to trap any fallen leaves and fragments of stems and branches. Seedlings from plants in each of these plots were threaded through netting covering the soil surface when they were about 4 cm tall. The netting was not unfolded to cover the plants until the lowermost leaves began to senesce so that any shading effect would be minimized. These plots were also harvested at reproductive maturity, but fallen material was collected from inside the netting at regular intervals throughout the pod filling period. Both biomass (reduced on average by 15.2%; $F = 8.44$; $P < 0.05$) and seed yield (reduced on average by 22.8%; $F = 5.12$; $P < 0.05$) were significantly smaller in the netted plots than in those plots without nets. The proportions of vegetation and pod material lost from each of the four genetic cohorts also differed significantly. Losses of pod and vegetative dry weights in the open plots was therefore estimated separately for each cohort, and as a respective proportion of material standing at reproductive maturity, by the following equation:

$$L = (DN/RN) \times R$$

Where L = estimated biomass lost, DN = mean biomass

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[1] Mention of trade names does not imply endorsement of or discrimination against any other product by the authors.

dropped from plants in the netted plots, RN = mean biomass recovered at reproductive maturity from the netted plots, and R = biomass recovered at reproductive maturity in each uncovered plot. The factors DN/RN were 1.77, 0.04, 0.14, and 0.14 for pods, and 0.54, 0.20, 0.47, and 0.38 for the vegetative tissues of the progenitors, landraces, pre-1980 cultivars, and modern genotypes, respectively. Harvest index was calculated by dividing the dry weight of seed by the dry weight of biomass after the estimated fallen material dry weight had been added to the actual values recorded.

Tissue N Analyses

Tissue samples for N analyses were collected from a single genotype from each cohort (i.e., Lo153, PI 181949, Chilean 78, and LC460266) sown at Pullman on 11 April 1997. Plot sizes, seeding rates, and plant husbandry were identical to those described previously. Two plants selected at random from each of three replicates (i.e., six plants in total) were sampled at 50% flowering and two others were taken at reproductive maturity again from each of three replicate plots for each of these four genotypes. Each plant sampled was partitioned into component organs, i.e., stems and leaves at 50% flowering; and leaves, fallen leaves, mainstems, branches, pods, and seeds at reproductive maturity. The dry weights of all components were determined and the elemental N concentration (mg g^{-1}) of each component organ was determined separately by combustion with a nitrogen determinator (Model FP420, Leco Corporation, St. Joseph, MI) (American Association of Cereal Chemists, 1995).

Statistical Analysis

Analysis of variance (ANOVA) was carried out on the combined data from the three experiments in a split-plot design with experiment as the main plot and cohorts–genotypes as the subplots with the SAS statistical package (SAS Institute, 1985). Analysis of variance was also carried out on data from each experiment separately. Comparisons between experiments and between individual cohorts–genotypes were made by least-squares means generated by the relevant ANOVA. Analyses of biomass and total N (i.e., biomass, residue production, pod wall, seed yield, biomass of fallen material and total

N ha^{-1}) were always carried out on data transformed to log_{10} ($x + 1$), and analyses of HI were performed on data transformed to arcsin x in order in both cases to improve homogeneity of the respective variances (Mead et al., 1993).

RESULTS

Environmental Conditions and Crop Phenology

Average crop durations (sowing until harvest maturity) were 91 ± 1, 99 ± 1, and 146 ± 1 d in Pullman 1996, Pullman 1997, and Reading 1997, respectively (Table 1). During these periods mean daily temperatures were substantially warmer in both years at Pullman than at Reading (Fig. 1): values throughout the entire crop duration were 16.1, 17.5, and 14.1°C for Pullman 1996, Pullman 1997, and Reading 1997, respectively, while those during the pre-flowering period averaged 13.4, 14.7, and 11.0°C, respectively. Minimum temperatures during pre-flowering period were below 0°C on 12 nights at Reading, but on only two nights at Pullman in 1997 and were above 0°C throughout this period at Pullman in 1996. Mean daily photoperiod during pre-flowering growth was longer at Pullman (where plots were sown later) than at Reading, averaging (inclusive of civil twilight) 16.8, 16.9, and 15.6 h d^{-1} for Pullman 1996, Pullman 1997, and Reading 1997, respectively. The average durations to flowering of the 12 genotypes were 55, 49, and 74 d after sowing for Pullman 1996, Pullman 1997, and Reading 1997, respectively, (Fig. 1; Table 1) and reflected the fact that photothermal conditions were more inductive at Pullman.

The rainfall received throughout crop duration at Pullman in 1997 (138 mm) was substantially more than that in 1996 (82 mm), but less than that at Reading (201 mm) (Fig. 1). However, mean daily rainfall throughout crop duration was similar in each of the 2 yr at Pullman (0.99 and 0.85 mm d^{-1} in 1996 and 1997, respectively), and was substantially less than that received at Reading

Table 1. Durations from sowing to 50% flowering, duration from sowing to reproductive maturity and reproductive duration of 12 genotypes of lentil and of the same genotypes grouped into cohorts.

Genotype	50% Flowering			Reproductive maturity			Reproductive duration		
	Pullman 1996	Pullman 1997	Reading 1997	Pullman 1996	Pullman 1997	Reading 1997	Pullman 1996	Pullman 1997	Reading 1997
					days				
Lo 153	51	46	68	95	97	138	50	51	70
Lo 56	57	53	74	85	98	147	37	46	73
Lo 4	52	51	71	93	100	143	47	49	72
PI 169527	55	46	75	94	100	145	43	54	70
PI 181949	59	47	75	91	101	144	37	54	69
PI 211732	56	48	77	86	99	144	33	51	67
Chilean 78	54	48	73	91	99	149	39	51	76
Tekoa	54	47	73	94	99	148	43	52	75
Laird	61	57	80	96	107	152	40	50	72
LC960254	54	45	73	86	96	139	35	51	66
LC460266	53	45	73	89	97	148	38	52	75
LC460199	56	52	77	89	98	149	36	46	72
Progenitors	53a†	50a	71a	92a	98a	143a	40a	49a	71ab
Landraces	57b	47a	76b	90a	100a	145a	34b	53a	69a
Older cultivars	56ab	50a	76b	94c	101a	150b	38ab	51a	74b
Modern germplasm	54a	47a	75b	88b	97b	145a	33b	50a	71ab
Root MSE	2.8	2.1	1.0	2.1	3.5	3.7	3.1	4.4	3.7

† Cohorts means within columns which share the same letter(s) are not significantly different at P = 0.05.

(1.32 mm d^{-1}) (Fig. 1). The Reading crop also received more rainfall during the reproductive period (148 mm or 1.74 mm d^{-1}) than did the plots at Pullman. Rainfall receipt during reproductive growth was however very different in the two Pullman experiments, i.e., a meager 7 mm (0.14 mm d^{-1}) in 1996 compared with 63 mm (0.99 mm d^{-1}) in 1997 (Fig. 1). Maximum temperatures during reproductive growth were very similar at Pullman in 1996 (averaging 27.9°C) and 1997 (27.8°C) and were much warmer than those at Reading (22.7°C). The 1996 Pullman crops were therefore subjected to terminal drought sooner and consequently matured earlier (on average after 91 d from sowing) than did those in 1997 (99 d) and especially so compared with Reading (146 d) (Fig. 1; Table 1).

Biomass Production and Residue Yield

Significant increases in biomass at reproductive maturity were found on moving from the progenitors (which averaged just 0.72 Mg ha^{-1} over all three experiments) to the landraces (3.51 Mg ha^{-1}), and from the landraces

to the older (pre-1980) cultivars (5.11 Mg ha^{-1}) in all three experiments ($P < 0.05$; Fig. 2). However, no further improvement in biomass was found on moving from the older cultivars to the modern germplasm (5.06 Mg ha^{-1}) in any of the three experiments, and at Reading in 1997, the biomass of the modern germplasm was no greater than that of the landraces (Fig. 2; Table 2).

Residue production (stems, leaves, and pods including dropped material, but excluding nodulated roots) was correspondingly smallest in the progenitors (which had a mean residue production averaged over the three experiments of just 0.61 Mg ha^{-1}). The landraces produced more residue (2.38 Mg ha^{-1}) than the progenitors ($P < 0.001$ in each experiment) but less than those of the older cultivars (3.79 Mg ha^{-1}; $P < 0.01$ at Pullman in 1996 and Reading in 1997, and $P < 0.001$ at Pullman in 1997) in all three experiments (Fig. 2). Residue production by the modern germplasm was less than that produced by the older cultivars in all three experiments (averaging 3.10 Mg ha^{-1}) (Fig. 2). This difference was
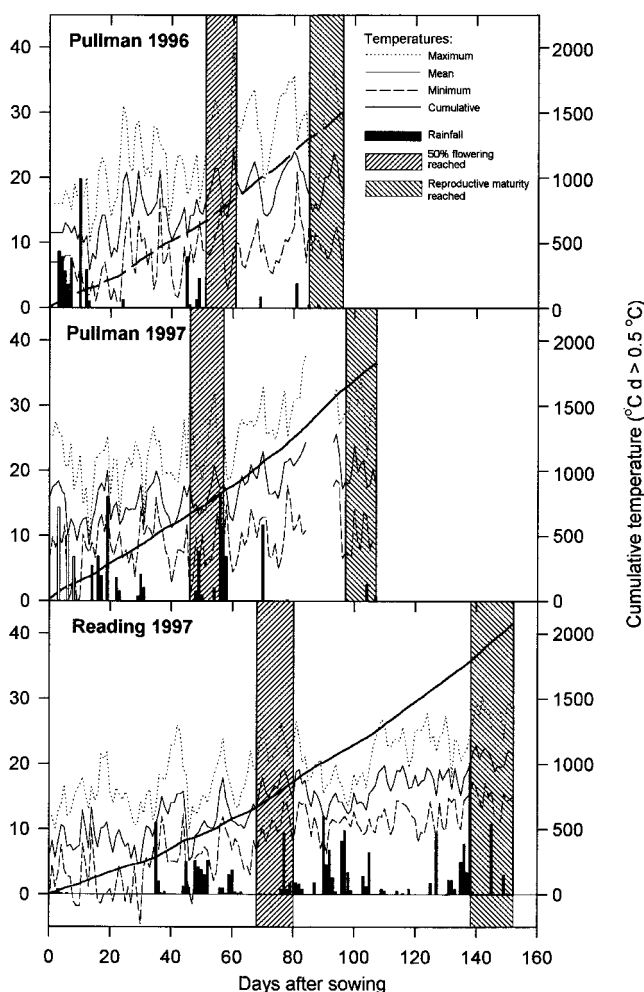

Fig. 1. Daily temperature mean, minimum and maximum temperature (°C), cumulative mean temperature above a base temperature of 0.5 °C (°C d) and daily rainfall (mm) at Pullman in 1996 and 1997 and at Reading in 1997. Open bars at Pullman in 1997 represent supplementary irrigation.
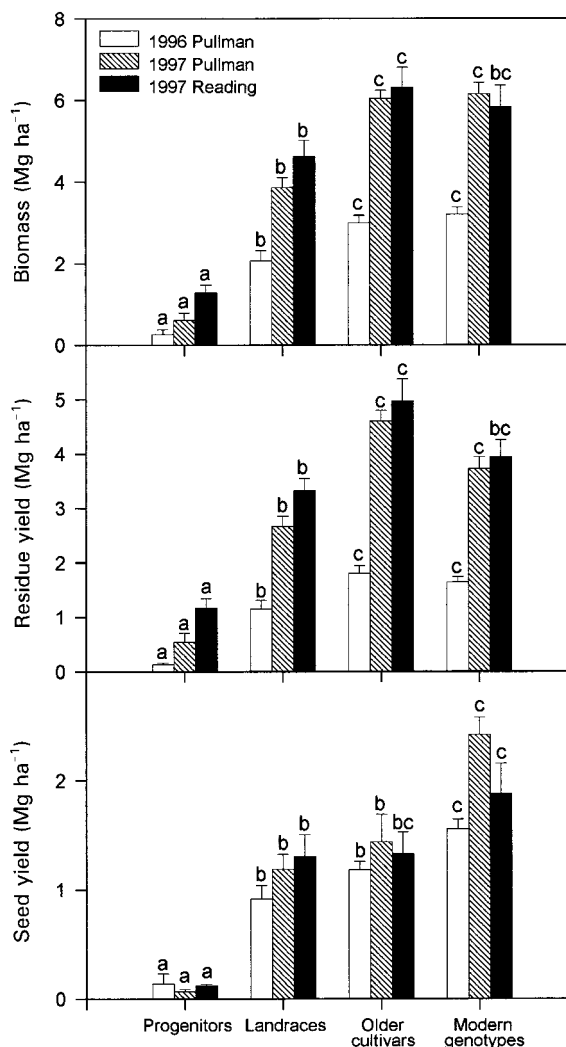

Fig. 2. Biomass, residue yield, and seed yield at reproductive maturity, including dropped seed, for four lentil cohorts. Component means represented by bars which share the same letters within each experiment (i.e., similarly shaded or open bars) are not significantly different at $P = 0.05$.

Table 2. Biomass, harvest index, residue yield, and seed yield at reproductive maturity of 12 genotypes of lentil. Material which fell from the plants before, but not during, harvest at reproductive maturity is included.

Genotype		Biomass			HI			Residue yield			Seed yield		
		Pullman 1996	Pullman 1997	Reading 1997	Pullman 1996	Pullman 1997	Reading 1997	Pullman 1996	Pullman 1997	Reading 1997	Pullman 1996	Pullman 1997	Reading 1997
							Mg ha^{-1}						
Progenitors	Lo153	0.60	1.30	1.99	0.56	0.07	0.08	0.23	1.20	1.82	0.37	0.10	0.17
	Lo56	0.10	0.33	0.85	0.14	0.09	0.08	0.08	0.28	0.79	0.01	0.04	0.07
	Lo4	0.10	0.43	1.01	0.29	0.21	0.12	0.07	0.35	0.88	0.03	0.08	0.13
Landraces	PI 169527	1.83	4.39	4.41	0.46	0.29	0.20	1.01	3.10	3.46	0.82	1.30	0.95
	PI 181949	2.10	3.51	5.26	0.37	0.24	0.29	1.35	2.67	3.69	0.75	0.85	1.57
	PI 211732	2.27	3.68	4.21	0.52	0.39	0.32	1.10	2.25	2.83	1.17	1.43	1.37
Older cultivars	Chilean 78	2.95	6.32	6.77	0.45	0.32	0.24	1.63	4.31	5.12	1.32	2.01	1.65
	Tekoa	2.52	6.08	5.61	0.39	0.29	0.24	1.53	4.34	4.24	0.99	1.74	1.37
	Laird	3.49	5.73	6.53	0.36	0.10	0.15	2.25	5.17	5.55	1.24	0.56	0.97
Modern germplasm	LC960254	3.11	6.43	2.89	0.50	0.35	0.33	1.55	4.15	1.46	1.56	2.28	1.43
	LC460266	2.89	6.15	7.07	0.49	0.42	0.35	1.46	3.61	4.55	1.43	2.55	2.52
	LC460199	3.60	5.85	5.99	0.47	0.41	0.27	1.92	3.42	4.34	1.68	2.44	1.65
Root MSE		0.58	0.63	1.23	0.10	0.07	0.06	0.33	0.47	0.74	0.29	0.36	0.59

not statistically significant in any single experiment, but became significant when data from all three experiments were combined ($P < 0.01$).
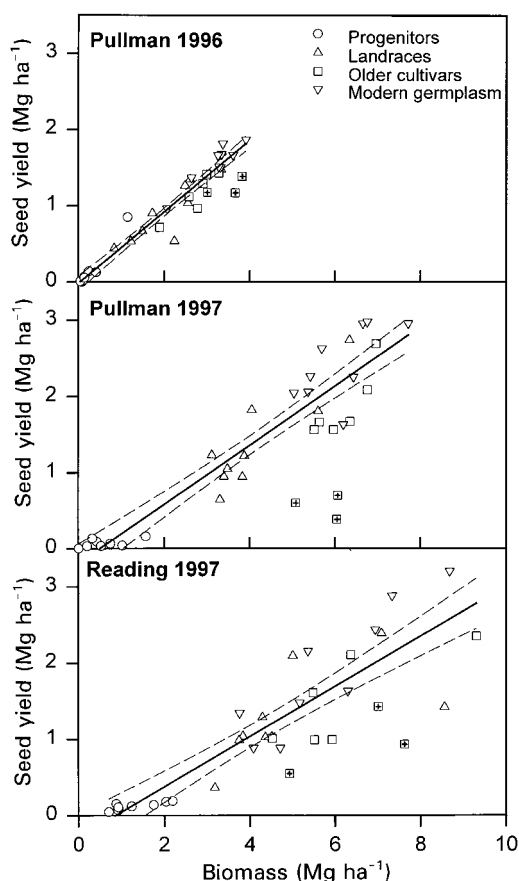
Biomass and residue production at Pullman in 1997

Fig. 3. The relation between seed yield and biomass at harvest maturity. Both axes are inclusive of material dropped before and during harvesting. Solid lines represent the least squares regressions for three replicate plots of all genotypes except for the outlying cv. Laird plots (see text) which are represented by a cross within the symbols. The regression lines have the equations $y = 0.468x - 0.016$ ($r^2 = 0.94$) for Pullman 1996, $y = 0.389x - 0.196$ ($r^2 = 0.88$) for Pullman 1997 and $y = 0.329x - 0.281$ ($r^2 = 0.79$). The broken lines represent the 95% confidence intervals for these regressions.

(averaging 4.27 and 2.95 Mg ha^{-1}, respectively) were much greater than those at Pullman in 1996 (2.13 and 1.18 Mg ha^{-1}, respectively) (Fig. 2; Table 2). This difference, we believe, may be explained in part by the slightly warmer temperatures (when averaged throughout crop duration) in 1997, but is more likely to reflect the higher rainfall, and especially that which fell during reproductive growth which encouraged continued branch production after flowering (Fig. 1). Biomass and residue yields were greatest at Reading in 1997 (averaging 4.51 and 3.35 Mg ha^{-1}, respectively; Fig. 2, Table 2) where plots received most rain and crop duration was longest.

The Relation between Seed Yield and Residue Yield

Seed yield was strongly and positively correlated with both biomass (Fig. 3) and residue yield (Fig. 4) in each experiment. In contrast, there is evidence that the increases in seed yield along the genetic gradient from progenitors to modern germplasm are related to relatively modest increases in HI (Tables 2 and 3). For example, averaged over the three experiments the HIs for progenitors, landraces, older cultivars, and modern breeding material were 0.19, 0.34, 0.28, and 0.40, respectively. There were, however, significant variations in the HIs of the 12 genotypes within each of the three experiments (Tables 2 and 3), and even between genotypes within the same cohort in both years at Pullman (Table 3). Furthermore, the mean HI across all genotypes was significantly different in each experiment and there was a significant interaction between experiment and genotype (Table 3) illustrating that environment and phenology play a large role in determining the HI of individual genotypes.

The phenology of the older cv. Laird was poorly adapted to the environmental conditions at both Pullman and Reading and this cultivar always flowered excessively late (Table 1). Cultivar Laird therefore had a large vegetative biomass at flowering, and consequently produced more residue at a smaller HI than all of the other cultivars in each of the three experiments (Table 2). The HI of cv. Laird was further reduced by its rela-
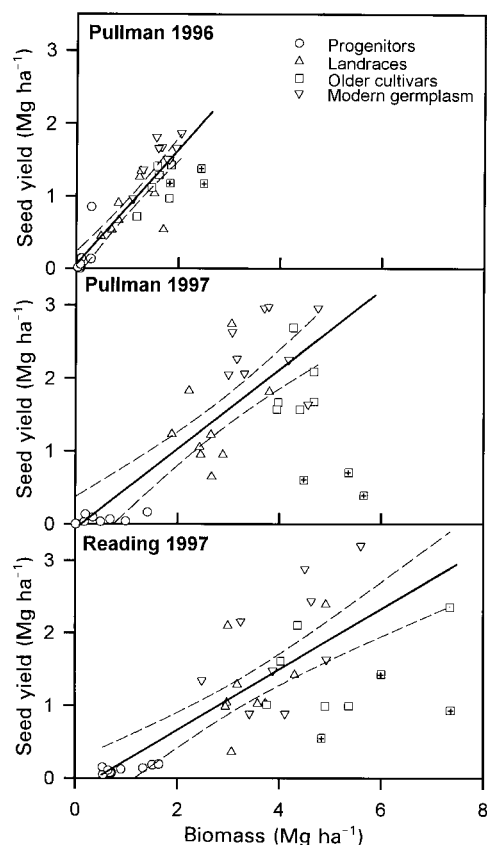
Fig. 4. The relation between seed yield and residue production at harvest maturity. Both axes are inclusive of material dropped before and during harvesting. Solid lines represent the least squares regressions for three replicate plots of all genotypes except for the outlying cv. Laird plots (see text) which are represented by a cross within the symbols. The regression lines have the equations $y = 0.798x - 0.056$ ($r^2 = 0.81$) for Pullman 1996, $y = 0.546x - 0.016$ ($r^2 = 0.68$) for Pullman 1997 and $y = 0.415x - 0.170$ ($r^2 = 0.62$). The broken lines represent the 95% confidence intervals for these regressions.

tively poor seed yields in comparison to the other older cultivars (Tekoa and Chilean 78) in both 1997 experiments (Table 2). In the 1996 Pullman experiment, cv. Laird performed relatively well in terms of seed yield in comparison with the other older and modern cultivars but seed yields were generally poor and vegetative growth was restricted by lack of soil moisture (Table 2; Fig. 1).

At Pullman in 1996, values of HI were relatively large and less variable than in the other experiments because vegetative growth was restricted by dry weather (Fig. 1; Table 2). In these circumstances, the relatively small mean HI of the progenitors (0.33) accounted for much of the overall variation in HI between cohorts, although it differed significantly from only the greatest HI achieved by the modern germplasm (0.49; $P < 0.05$). The mean HI of the landraces (0.45) and the older cultivars (0.40) did not differ significantly from those of either the progenitors or the modern germplasm. Production of vegetative biomass increased in 1997 by a much greater proportion than did seed yield compared with 1996 (Fig. 2). Harvest indices were consequently smaller in 1997 (Table 2). The HI of the modern germ-

plasm (0.40 at Pullman and 0.31 at Reading) were significantly greater in 1997 than those of the older cultivars at both locations (0.23, $P < 0.001$ at Pullman and 0.21, $P < 0.05$ at Reading), but greater than the landraces only at Pullman (0.31, $P < 0.05$ at Pullman and 0.27, $P > 0.05$ at Reading). There was no difference in the HIs of the older cultivars and landraces at either location in 1997.

Seed Yield

Seed yields have improved consistently on moving along the gradient from the progenitors, which had meager average yields (including fallen seed) of just 0.11 Mg ha^{-1} over the three experiments, towards modern germplasm (1.95 Mg ha^{-1}) (Fig. 2). In all three experiments, the mean seed yield of progenitors was less than that of landraces which was less than that of older cultivars which was less than that of modern germplasm (Fig. 2). The greatest improvements in seed yield were made on moving from progenitors to the landraces (from 0.11–1.13 Mg ha^{-1} over the three experiments, a more than 10-fold increase). The mean seed yields of progenitors and landraces differed significantly in all three experiments ($P < 0.001$).

Substantial increases in seed yield have also been made during the past two decades as a result of lentil breeding. The three modern genotypes out-performed all others in terms of seed yield in both years at Pullman (Table 2). The modern breeding line LC460266 produced the most seed when most rain fell, but had smaller yields than the other two modern genotypes in the driest circumstances (Pullman 1996) (Table 2). At Reading in 1997, the older cultivar Chilean 78 performed relatively well and out yielded both cv. Mason (LC960254) and accession LC460199 (Table 2). Accession PI 181949 also out yielded cv. Mason in this experiment. The mean seed yields of older cultivars were significantly smaller than those of the modern germplasm at Pullman in 1996 (1.18 and 1.56 Mg ha^{-1}, respectively; $P < 0.05$) and again in 1997 (1.43 and 2.42 Mg ha^{-1}, respectively; $P < 0.001$). A similar relative increase in the mean yields of modern germplasm (1.88 Mg ha^{-1}) over older cultivars (1.33 Mg ha^{-1}) was almost significant in Reading ($P = 0.07$) (Fig. 2). Although the mean seed yields of the older cultivars were greater than those of the landraces in all experiments (Fig. 2), these increases were relatively modest, and statistically insignificant (means did not differ at $P = 0.05$). Genotypes within cohorts differed significantly in seed yield in 1997 at both Pullman and Reading (Table 2 and Table 3).

Loss of Plant Material before Reproductive Maturity

Substantial losses of biomass occurred towards the later stages of pod filling as the plants senesced (Fig. 5). These losses were greatest in the older cultivars and modern germplasm which were almost leafless by reproductive maturity. When those losses which occurred during harvesting are included, the total biomass lost amounted to 0.17 Mg ha^{-1} for Lo153, 0.48 Mg ha^{-1} for

Table 3. Sums of squares from the analyses of variance for biomass, harvest index (HI), residue yield, and seed yield for 12 genotypes of lentil. Seed yield, residue yield and biomass data were transformed to $\log_{10}(x+1)$ and HI data to arcsin x before analysis.

	Experiment			Between Genotype			Between Cohort			Within Cohort			Experiment × Genotype			Experiment × Cohort		
	SS†	F-value	P	SS	F-value	P	SS	F-value	P	SS	F-value	P	SS	F-value	P	SS	F-value	P
Pullman 1996																		
Biomass				1.70	21.7	***	1.62	66.8	***	0.09	1.51	ns						
HI				0.52	4.98	***	0.14	0.09	ns	0.38	4.96	**						
Residue yield				0.92	19.7	***	0.87	62.5	***	0.05	1.40	ns						
Seed yield				0.70	14.6	***	0.65	42.9	***	0.05	1.56	ns						
Pullman 1997																		
Biomass				2.51	69.2	***	2.42	138.1	***	0.09	3.45	*						
HI				0.51	8.63	***	0.35	12.2	***	0.17	3.84	**						
Residue yield				1.74	46.3	***	1.63	85.3	***	0.11	3.93	**						
Seed yield				1.27	39.2	***	1.10	46.7	***	0.17	7.11	***						
Reading 1997																		
Biomass				1.62	23.7	***	1.49	54.5	***	0.14	2.72	*						
HI				0.31	8.02	***	0.25	18.5	***	0.06	2.11	ns						
Residue yield				1.15	25.6	***	1.01	45	***	0.14	4.22	**						
Seed yield				0.89	8.86	***	0.80	27.5	***	0.09	1.24	ns						
All Experiments																		
Biomass	1.28	56.0	**	5.63	91.7	***	5.39	233.9	***	0.24	5.06	***	0.18	1.46	ns	0.10	2.18	ns
HI	0.83	26.6	**	1.01	14.9	***	0.70	20.9	***	0.30	6.29	***	0.33	2.41	**	0.03	0.44	ns
Residue yield	1.76	265.8	***	3.62	83.8	***	3.41	184.1	***	0.21	6.41	***	0.18	2.09	*	0.09	2.45	*
Seed yield	0.06	1.62	ns	2.62	43.2	***	2.47	109.3	***	0.15	3.19	***	0.22	1.79	*	0.06	1.33	ns

\# Sum of squares taken from the relevant ANOVA.
*, **, *** Indicate significance at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

PI 181949, 1.13 Mg ha^{-1} for Chilean 78, and 1.07 Mg ha^{-1} for LC460266: these values represented 75, 13, 30, and 25% of biomass recovered at mature harvest, respectively. All of the progenitors were strongly indeterminate and also had pods which shattered as they approached reproductive maturity. A large number of seeds, and some pods, therefore fell from the progenitors before the stage at which 90% of the pods had
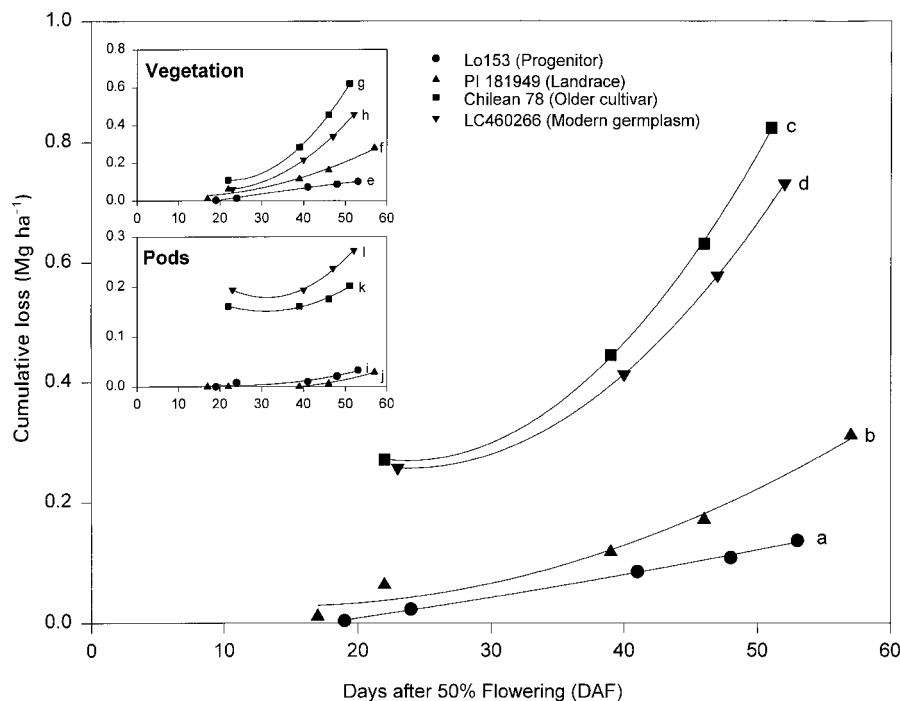

Fig. 5. The biomass and dry weights of vegetative and pod material (inset) lost from plants in netted plots sown at Pullman on 12 May 1997. Solid lines represent polynomial regressions for three replicate plots which have the equations:

a. $y = -0.049 + 2.486 \times 10^{-3} x + 1.793 \times 10^{-5} x^2$ $(R^2 = 0.998)$; **b.** $y = 0.060 - 4.396 \times 10^{-3} x + 1.526 \times 10^{-4} x^2$ $(R^2 = 0.978)$; **c.** $y = 0.688 - 0.035x + 7.424 \times 10^{-4} x^2$ $(R^2 = 1.000)$; **d.** $y = 0.595 - 0.028x + 5.969 \times 10^{-4} x^2$ $(R^2 = 1.000)$; **e.** $y = 0.069 + 3.961 \times 10^{-3} x - 1.351 \times 10^{-5} x^2$ $(R^2 = 0.995)$; **f.** $y = 0.0302 - 2.040 \times 10^{-3} x + 1.117 \times 10^{-4} x^2$ $(R^2 = 0.978)$; **g.** $y = 0.414 - 0.027x + 6.153 \times 10^{-4} x^2$ $(R^2 = 1.000)$; **h.** $y = 0.205 - 0.015x + 3.792 \times 10^{-4} x^2$ $(R^2 = 1.000)$; **i.** $y = 0.023 - 1.697 \times 10^{-3} x + 3.488 \times 10^{-5} x^2$ $(R^2 = 0.922)$; **j.** $y = 0.031 - 2.436 \times 10^{-3} x + 4.189 \times 10^{-5} x^2$ $(R^2 = 0.982)$; **k.** $y = 0.269 - 7.607 \times 10^{-3} x + 1.228 \times 10^{-4} x^2$ $(R^2 = 0.987)$; **l.** $y = 0.395 - 0.014x + 2.220 \times 10^{-4} x^2$ $(R^2 = 0.997)$.

Table 4. Total N concentration (mg g⁻¹ dry weight) of component organs at flowering and at maturity.

| Genotype | At flowering | | | At reproductive maturity | | | | |
	Leaf	Stem	Vegetation	Leaf	Mainstem	Branches	Pod	Seed
				mg g⁻¹				
Lo153	39.7 ± 1.7†a‡	19.7 ± 2.1a	35.7 ± 2.2a	18.5 ± 2.9a	16.7 ± 0.8a	20.5 ± 1.2a	9.2 ± 1.5ab	44.3 ± 0.6a
PI 181949	38.5 ± 1.9a	18.3 ± 1.6a	31.4 ± 1.2ab	14.9 ± 0.7a	8.2 ± 0.4b	13.0 ± 1.5b	10.0 ± 2.6a	42.2 ± 1.6a
Chilean 78	35.9 ± 2.1a	18.0 ± 0.8a	27.3 ± 1.8b	15.5 ± 0.8a	8.9 ± 0.7b	10.9 ± 1.1b	4.5 ± 0.5b	44.2 ± 0.8a
LC460266	40.8 ± 1.2a	21.8 ± 2.0a	32.0 ± 1.6ab	18.2 ± 0.6a	8.2 ± 1.1b	10.8 ± 1.3b	6.8 ± 0.6ab	43.2 ± 1.0a

† Standard Error of the Mean, $n = 6$.
‡ Means within columns which share the same letter are not significantly different at $P = 0.05$.

turned golden brown and the plants were considered mature for the purpose of harvesting. In the Lo153 plots seeds and pods with a dry weight equivalent to 0.06 Mg ha⁻¹ [or 177% of the weight of (mostly empty) pods harvested at reproductive maturity] were shed from plants before reproductive maturity. The more domesticated genotypes shed less seed through pod dehiscence. Nevertheless a substantial quantity of pod and seed material fell from all genotypes: equivalent to 4, 14, and 14% of the pod (including seed) material recovered at reproductive maturity for PI 181949, Chilean 78, and LC460266, respectively.

Nitrogen Accumulation and Partitioning

The N concentrations in seeds were similar in all of the four genotypes sampled and there was no evidence that values had changed as a consequence of selection for seed yield (Table 4). Similarly, in all of the genotypes studied, leaf N concentrations were significantly greater at flowering than at reproductive maturity ($F = 211.7$; $P < 0.001$) indicating that leaves were losing N, probably as a result of reallocation to seed, during pod filling. By reproductive maturity even those leaves which remained attached to the plants of genotypes other than the progenitors were no longer green. The concentrations of N within attached (Table 4) and fallen leaves (21.4, 19.1, 16.1, and 17.3 mg g⁻¹ for Lo153, PI 181949, Chilean 78, and LC460266, respectively) were therefore similar in all of the four genotypes. The N concentrations of stems and branches were smaller than those of leaves at flowering, and also declined during pod filling. At the time of reproductive maturity, the N concentrations of the mainstem and branches had declined to

values smaller than those of the leaves and were especially depleted in the mainstem tissue (Table 4). While the N concentrations of the stem and branches of PI 181949, Chilean 78 and LC460266 were similar at both flowering and reproductive maturity the values for the progenitor Lo153 remained greater than those of the other three genotypes at reproductive maturity suggesting a less efficient mobilization of N from stems and branches into seed (Table 4).

Samples for total N analyses were taken from plots sown on 11 April 1997 at Pullman which produced greater biomass and seed yield than those sown on 9 May 1996 and 12 May 1997 in Pullman, and on 21 March 1997 in Reading (Table 2, Table 5). Biomass productivity was generally impressive in these early-sown plots and also reflected the pattern previously seen in which the modern cultivar (LC460266) produced less residues than the older cultivar (Chilean 78) but more than the landrace (PI 181949) and much more than the progenitor (Lo153) (Table 5). Since the N concentration of seed was similar in the four genotypes studied the quantity of N harvested in seed was almost entirely determined by seed yield and was therefore greatest for the most productive cv. Chilean 78 (185.8 kg N ha⁻¹, Table 5).

In these plots, HI increased along the genetic gradient as selection for seed yield intensified (Table 5). The N harvest indices (NHI), i.e., the proportion of total N within above-ground biomass (excluding shed senesced leaves) harvested in seed, were much greater than the proportion of above-ground biomass which was harvested in seed (HI) in all four genotypes (Table 5). The NHI also increased substantially throughout domestication: from 0.35 for Lo153 to 0.85 for LC460266 (Table

Table 5. Total N and dry matter of component organs of four genotypes of lentil at flowering and at maturity, plots sown on 11 April 1997 at Pullman.

| Genotype | Flowering | Reproductive maturity | | | | | | | |
	Vegetation	Leaf	Stem	Pod	Litter	Residue	Seed	Biomass	N harvest index
					Total N (kg ha⁻¹)				
Lo153	1.3 ± 0.3a	5.0 ± 1.1a	9.8 ± 2.4a	5.3 ± 0.9a	5.7 ± 0.1a	20.1 ± 1.7a	12.8 ± 2.0a	32.2 ± 2.5a	0.35 ± 0.05a
PI 181949	26.0 ± 5.2b	10.7 ± 2.8a	12.7 ± 0.8a	10.0 ± 2.6b	9.7 ± 0.4ac	33.3 ± 3.7b	103.8 ± 12.8b	137.0 ± 12.0b	0.75 ± 0.04b
Chilean 78	32.0 ± 4.3b	10.3 ± 3.0a	20.7 ± 2.6b	8.3 ± 0.8ab	23.1 ± 0.3b	39.5 ± 4.4b	185.8 ± 26.2c	225.7 ± 26.7c	0.81 ± 0.03bc
LC460266	40.2 ± 6.7b	5.5 ± 1.6a	13.5 ± 2.6a	8.2 ± 0.7ab	13.1 ± 0.9c	27.3 ± 3.3a	150.3 ± 6.7c	177.5 ± 8.3bc	0.85 ± 0.01c
					Dry matter (kg ha⁻¹)				
Lo153	37 ± 6a	2474 ± 418a	1000 ± 281a	660 ± 155a	112 ± 40a	4 134 ± 813a	284 ± 35a	4 419 ± 827a	0.07§ ± 0.01a
PI 181949	952 ± 114b	6439 ± 292b	1531 ± 73b	1073 ± 109b	405 ± 24b	9 044 ± 372b	2442 ± 283b	11 486 ± 523b	0.21 ± 0.02b
Chilean 78	1243 ± 30bc	9860 ± 882c	2339 ± 230b	1921 ± 173c	861 ± 59c	14 121 ± 1215c	4225 ± 623c	18 347 ± 1612c	0.23 ± 0.02bc
LC460266	1305 ± 114c	6955 ± 122b	1675 ± 271b	1224 ± 48b	764 ± 53c	9 855 ± 302b	3482 ± 141c	13 337 ± 261b	0.26 ± 0.01c

† Standard Error of the Mean, $n = 3$.
‡ Means within columns which share the same letter are not significantly different at $P = 0.05$.
§ Harvest Index.

5), suggesting that future improvements may be constrained more by N nutrition than by C metabolism. Despite these increases in NHI, the potential net gain in soil N when residues were incorporated into soil after the harvest of seed doubled along the gradient from about 20 kg N ha^{-1} for Lo153 to almost 40 kg N ha^{-1} for Chilean 78 (Table 5) because of improved residue production (4.13 Mg ha^{-1} for Lo153 to 14.1 Mg ha^{-1} for Chilean 78, Table 5).

DISCUSSION

Lentil crop improvement has led to consistent increases in both biomass production and seed yield. A strong and positive correlation between seed yield and biomass, similar to that reported by Erskine (1983) for 3586 accessions in what was at that time the world lentil germplasm collection grown in Syria, was found whenever the genotypes investigated here were phenologically suited to their production environment. The production of vegetative biomass is correlated positively with seed yield because more reproductive nodes are available on taller and more bushy plants, and because additional photosynthetic capacity from a more leafy canopy is available to meet the increased demands for carbon assimilate for DM accumulation and N$_2$ fixation, especially after flowering.

Improvements in HI achieved along the genetic gradient from the landraces to the modern genotypes have been modest; values are inconsistent and strongly influenced by environment. Sinha et al. (1982) hypothesized that the HI of grain legume crops will always tend to be smaller than those of cereals because of the greater energy costs of synthesizing protein-rich seeds. Nevertheless, relatively large HI values have been reported for many grain legumes, e.g., 0.46 for productive (2.8 Mg seed ha^{-1}) autumn-sown lentil in New Zealand (McKenzie and Hill, 1990), 0.35 to 0.53 for soybean [*Glycine max* (L.) Merrill; Schapaugh and Wilcox, 1980], and 0.44 to 0.64 for determinate cowpea [*Vigna unguiculata* (L.) Walp.; Fernandez and Miller, 1985].

The HIs recorded in the experiments reported here varied greatly between genotypes grown in the same conditions, and between genotypes of the same cohort. Harvest index was also strongly affected by environment: values were much greater at Pullman in 1996 (averaging 0.42), under conditions in which vegetative growth was restricted by limited soil moisture, and much smaller under the relatively cool and damp conditions experienced at Reading (averaging 0.22), where vegetative growth was much greater. However, under the wetter conditions experienced at Pullman in 1997, the effects of drought stress were reduced and genetically controlled variations in HI became more apparent. In these circumstances, HI increased on moving along the genetic gradient towards modern germplasm.

Seed yield in lentil is dependent upon the production of nodes and the proportion of them which become reproductive. Notwithstanding the strong positive relation between above-ground biomass and seed production during domestication (Fig. 3), it remains possible

that HI could be increased and seed yields consequently further improved by the selection of more determinate genotypes in which the flowering period is condensed and a greater proportion of nodes bear pods. In such genotypes, assimilates are partitioned to pods, rather than to continued vegetative growth and the production of late pods which may not produce mature seed by the time of harvest. Selection for early flowering is also likely to increase HI by increasing the proportion of crop duration during which pods are filling and through the avoidance of late-season drought (Erskine, 1983; Silim et al., 1993). However, since seed yield is dependent upon DM accumulation (Lawn, 1989), these approaches have obvious limits. Seed yield can only be maintained in increasingly early cultivars through more rapid pre-flowering biomass accumulation, which will tend to reduce HI (Whitehead et al., 1998). It is fortunate that the advantageous correlation between seed yield and biomass production shows no sign of deviation from traditional trends (Fig. 3).

The shedding of seeds from the dehiscing pods of the progenitors and the loss of intact pods or seed from shattering pods of other genotypes shortly before reproductive maturity tended to cause underestimations of both seed yield potential and HI. The further loss of biomass because of the senescence and drop of leaves during the later stages of pod filling was also substantial. Losses of vegetation similar to those reported here have been reported in many other grain legumes and have led to under-estimates of total biomass production and over estimates of HI (Hay, 1995). For example Khanna-Chopra and Sinha (1987) found that leaves and petioles constituting 20 to 30% of total DM were lost from a crop of chickpea (*Cicer arietinum* L.). Schapaugh and Wilcox (1980) compared the harvest indices obtained by either including or excluding fallen leaves and petioles in a two-year study of 24 cultivars of soybean and found a strong positive correlation between the two methods ($r = 0.96$ and 0.99). When comparing the performance of different genotypes under the same conditions it may well be sufficient to disregard fallen vegetation and to make comparisons on the basis of material recovered at harvest. However, in circumstances where environmental conditions influence rates of leaf senescence and/ or seed loss differentially, i.e., where some genotypes are inclined to lose more vegetation or seed than others (as is the case for seed loss from progenitors of lentil), or where the production of vegetative biomass per se is important it is impossible to ignore the fallen material. Some physiologists have therefore chosen to present their data in terms of maximum total DM production, i.e., absolute maximum biomass as distinct from recoverable biomass at reproductive maturity (see McKenzie and Hill, 1990). We too have estimated the amount of material lost on the basis of the collection of material from a number of netted plots.

Given the large N requirement for seed production the potential net soil N gain resulting from the incorporation of lentil residues in this experiment was modest. The maximum amount of N returned to the soil was 39.5 kg N ha^{-1} from the residues of cv. Chilean 78. This

value is similar to previously reported figures for lentil, e.g., 40 to 80 kg N ha^{-1} (Cowell et al., 1989; van Kessel, 1994; Kurdali et al., 1997). The potential N returned to the soil (excluding that from senescing nodulated roots, which remains to be quantified) was a function of the DM of residue returned to soil and therefore seems likely to increase as seed yield, and therefore biomass increases (Table 5).

The concentrations of N in lentil seeds, stems, and leaves reported here are similar to those cited previously (40, 11, and 28 mg g^{-1}, respectively; Kurdali et al. 1997). The proportion of N partitioned to seed at reproductive maturity (i.e., NHI) consistently exceeded the proportion of DM partitioned to seed HI in the four genotypes studied. Furthermore, the rate at which NHI increased along the genetic gradient was greater than the rate at which HI increased and was associated with greater depletions of N from stems and pod wall tissues of those mature plants which produced the best seed yields. A greater proportion of leaf material was lost from cultivars than from landraces perhaps because they began to remobilize N-based resources from leaves and stems in order to support pod growth earlier in the reproductive growth period, and did so at a greater rate. The N concentrations of dead leaves which remained attached to the mature cultivars and of leaves which had died and fallen from those plants were similar, suggesting that further N cannot be remobilized from leaf tissue. This finding, together with the increasing depletion of N from stems and pod wall along the gradient combine to indicate that NHI in lentil is unlikely to increase significantly in the future.

In his recent review, Sinclair (1998) concluded that the historical increase in the HI of grain crops may be a consequence of their increased ability to accumulate N as much as their improved partitioning of biomass. However, efforts to increase N accumulation in lentil from sources other than N$_2$ fixation are likely to prove difficult given the inhibition of N$_2$ fixation by inorganic N fertilizer, the use of which rarely leads to substantial yield increases (Bremer et al., 1989). It is possible, although a daunting prospect in many of the situations in which lentil is grown, that lentil seed yields could be improved by increasing N$_2$ fixation efficiency through the introduction of improved cultivars, the improved efficiency of the lentil-rhizobium symbiosis, or through the development of better inoculation protocols which might take advantage of improved strains of rhizobium (Sanoria and Mallik, 1981; Bremer et al. 1989). However, in agreement with Lawn (1989), we conclude that the ability of lentils to accumulate yet more N could limit future improvements in HI and seed yield.

Improvements in both seed yield and biomass have accelerated in the last 20 yr because of a growing commitment to lentil breeding. Prospects for further gains facilitated by a rapidly improving knowledge of lentil genetics. The need to provide numerous reproductive nodes, and the increasing requirement for photosynthetic capacity in order to sustain the rates of N and DM accumulation which will be necessary if seed yield is to be increased further, suggest that it may be difficult

to continue to improve lentil HI, and especially NHI. Nevertheless, there is, to date, no sign of a *yield plateau* for lentils (Fig. 2) and so it seems that prospects for further improved biomass and seed yield are good. Furthermore, the advantageous relation between seed and residue production seems likely to continue as lentils undergo further crop improvement. Thus, the potential of lentil to provide straw for feed and/or the residues needed to help in the restriction of soil erosion should also continue to improve in the years ahead.

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Effects of Phosphorus and Water Supply on Yield, Transpirational Water-Use Efficiency, and Carbon Isotope Discrimination of Pearl Millet

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ABSTRACT

Several studies have identified low soil P and water availability as major constraints to pearl millet [*Pennisetum glaucum* (L.) R. Br.] production in semi-arid West Africa. To evaluate the effects of phosphate and water supply on yield, transpirational water-use efficiency (WUE$_T$), and carbon-isotope discrimination (Δ), two varieties of pearl millet were cultivated in pots in a glasshouse at the ICRISAT Sahelian Centre, near Niamey, Niger. Phosphate and water supply had significant effects on yield, WUE$_T$, and Δ. Compared with the control plants, which had adequate water and P availability, yield was reduced 34% by low water supply and 48% by low P supply. Under high P-supply, water stress increased WUE$_T$ by approximately 37%. Under low P-supply, no effect of water supply on WUE$_T$ was observed. Water stress increased Δ by approximately 0.6‰ for low P plants, and 0.9‰ for high P plants. Added P increased Δ by 0.3 to 0.4‰. WUE$_T$ and Δ did not differ significantly between varieties. Differences in Δ between green and necrotic leaves were found within both P treatments under low water supply. We attribute changes in Δ to changes in the ratio of external to internal concentration of CO$_2$, (p_i/p_a), leakage rates of CO$_2$ out of bundle-sheath cells, respiration rates, or chemical composition of the plant material.

PEARL MILLET production systems of the West African Semi-Arid Tropics (WASAT) are characterized by low soil productivity and chronically low water supply (Payne, 1997). On-farm yields of pearl millet are usually very low (400–600 kg ha^{-1} of grain), but fertilization may increase yield to as much as 2500 kg ha^{-1} (McIntire and Fussell, 1989; Christianson et al., 1990). Generally, low yields are accompanied by low evapotranspirational water-use efficiency, which is brought about by a combination of low leaf area index and, for many environmental stresses, changes in WUE$_T$.

The dependence of WUE$_T$ on water- and nutrient supply has been demonstrated for various C$_3$ plant species, including wheat (*Triticum aestivum* L.; Farquhar and Richards, 1984), barley (*Hordeum vulgare* L.; Hubick and Farquhar, 1989), peanuts (*Arachis hypogaea* L.; Hubick et al., 1986), and sunflower (*Helianthus*; Virgona and Farquhar, 1996). Although less pronounced, WUE$_T$ of C$_4$ plants also appears to be affected by water and nutrient supply (Schenk and Barber, 1979; Onken and Wendt, 1989; Payne et al., 1992, 1995). Changes in WUE$_T$ reflect changes in stomatal conductance and/or internal capacity for CO$_2$ fixation, the latter being affected by enzyme activity (von Caemmerer et al., 1997) and plant nutrient status (Payne et al., 1992; Ranjith et al., 1995).

A correlation has been observed between discrimination against ^{13}C (Δ) and WUE$_T$. According to Farquhar (1983), Δ is mainly caused in C$_3$ species by (i) fractionation due to CO$_2$ diffusion (a); (ii) changes in stomatal resistance or assimilation rate, which affect the ratio of internal to ambient concentration of CO$_2$ (p_i/p_a); and (iii) fractionation (b_3) by the enzyme ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco).

For C$_4$ species, Δ is further affected by initial fixation of CO$_2$ (b_4) by the enzyme phosphoenolpyruvate carboxylase (PEPC), and "leakiness" (Φ) of CO$_2$ from bun-

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Abbreviations: DAS, days after sowing; DM, dry matter; Rubisco, ribulose-1,5-bisphosphate carboxylase-oxygenase; PEPC, phosphoenolpyruvate carboxylase; WUE$_{T,S}$, transpirational water-use efficiency, based on shoot dry matter; WUE$_{T,SR}$, transpirational water-use efficiency, based on shoot and root dry matter; Δ, carbon-isotope discrimination; p_i/p_a, ratio of external to internal concentration of CO$_2$.